PROCEEDINGS

OF THE

CALIFORNIA ACADEMY OF SCIENCES

Fourth Series

Vol. XXV, No. 9, pp. 235–244, 6 text figures June 1, 1944

ALICE EASTWOOD
SEMI-CENTENNIAL PUBLICATIONS

No. 9

THE PERENNIAL SOUTHWESTERN DATURA AND THE VALIDITY OF MATTHEW'S HYPOTHESIS IN PLANT GEOGRAPHY

BY

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Evidences of phylogeny among major plant groups rest upon two lines of observational research, viz., comparative morphology and paleobotany, and upon two methods of experimental research, viz., serum diagnosis and cytogenetics. Among species within a single genus evidences of phylogeny rest again upon comparative morphology in the broadest sense, along with breeding experiments and cytogenetics, with either supporting evidence or the lack of it from the fields of ecology and plant geography. Interpretation of morphology is thrown into sharper perspective by subjecting the data to Haeckel's Biogenetic Law, Dollo's Law of Irreversibility, Darwin's evolutionary theory, Liebig's Law of the Minimum as applied to distribution problems, Good's Theory of specific tolerance, Jordan's Law of Geminate Species, Eames' concept of "phyletic slides" within plant groups, and what I have chosen to call Matthew's Hypothesis of Peripheral Populations. The subject of the present paper is a consideration of Matthew's Hypothesis as it may prove valid in interpreting distribution phenomena in *Datura meteloides* DC.

In his now classic paper entitled "Climate and Evolution" (1915) the American vertebrate paleontologist, W. D. Matthew, presented a working hypothesis for the evolution of the higher vertebrates. He devoted three paragraphs in the beginning to his "Principles of Dispersal," with which we are chiefly concerned. His evolutionary theory embraced the concept that the evolution of land life has responded in adaptation to recurrent periods of aridity

through geologic time. In short, Matthew demonstrated that the major advances of vertebrate evolution have coincided with shifts in megaclimates, especially those shifts toward increasing aridity. It is a significant corollary of Matthew's Hypothesis, in my opinion, that the angiosperms of arid and semi-arid regions exhibit conspicuous evolutionary advance in their morphology over their relatives of mesic regions.

Matthew's Hypothesis

Matthew's Hypothesis holds that,

> *at any one time in the evolution of a taxonomic group the most advanced stages should be nearest the center of dispersal, the most conservative stages farthest from it.*

Or, to use the words of another vertebrate paleontologist, Prof. R. S. Lull, it may be stated that,

> "the most ancient members of a group are not to be found at the old center of evolution, but rather at the periphery of their migratory area." (Lull in George A. Baitsell, ed., Evolution of Earth and Man, pp. 118–119. 1929.)

In his original paper Matthew points out that the evolution of a race "should be at first most progressive at its point of original dispersal, and it will continue this progress at that point in response to whatever stimulus originally caused it and spread out in successive waves of migration, each wave a stage higher than the previous one" (1915, 180). Assuming that a species is the product, in part, of its environment, and that environments are subject to change, "it is the environment itself, biotic as well as physical, that migrates, and primitive species are those which have followed it, while those which remained have had to adapt themselves to a new environment and become altered thereby." However, it should be remembered that probably "it is never the case that the environment of the marginal species is an absolute replica of the older environment of the race" (1915, 180–181).

The American plant ecologist Stanley Cain expressed the concept in 1940 as follows: "in wide-ranging species populations mere distance constitutes a type of isolation and marginal or other portions of a population are frequently recognizable . . . without the development of any conspicuous discontinuity" (1940, 214). Cain points out, furthermore, that these marginal populations are genetically more homozygous. In the instance of *Datura meteloides,* the native solanaceous perennial known by the Indian name "tolguacha," this homozygosity may be demonstrated by the occurrence of distinctive leaf types of representative individuals from geographically marginal populations, as recorded in some of the larger herbaria.

Materials and Procedure

This study of *Datura meteloides,* it should be pointed out at the outset, is based wholly upon herbarium specimens and is subject to confirmation from an even more statistical approach, especially in the field over the extensive geographic range of the species, in the manner of Fassett's "mass collection"

studies (1941). It may be of interest to record how this problem arose. De-Candolle's original description of *Datura meteloides* rests, not upon the usual preserved herbarium "type" specimen but upon a Sesse and Mociño drawing, rather unfortunate for having been hastily copied from the original. The plant from which the drawing was made was collected at an unrecorded local-

Fig. 1. Maximum natural range (generalized) of *Datura meteloides* DC.

ity in, probably, central Mexico by Mociño. By comparing this drawing with modern herbarium collections as to close similarity of leaf blade outline an attempt was made to fix, in a general way at least, the possible geographic source, that is, a putative "type locality," of the material which served as the basis of what must be considered, in lieu of an actual preserved plant, the type of the species. The taxonomic history of this plant, and certain problems in the systematics of it, are treated elsewhere by the present author (1944).

This paper, then, arose from an examination of nearly 300 collections, primarily from two large herbaria, the U. S. National Herbarium, and the Rocky Mountain Herbarium of the University of Wyoming, with subsequent examinations of materials in the herbaria of the Academy of Natural Sciences at Philadelphia and the Field Museum. To the curators of these collections I am grateful for the privilege of studying the materials in their charge. The collections were sorted according to closeness of fit in leaf blade configuration. Four chief repetitions in leaf-form were encountered. These characteristic infraspecific variations in leaf-form—including equilateral and inequilateral, serrate and subentire forms—were then plotted on outline maps according to the place of collection as recorded on the herbarium labels of each. Mature leaves were chosen from each sheet and tracings were made of representative collections. Almost invariably the collections were of flowering specimens, and the leaves, therefore, associated with flowering shoots. It was found that those collections showing closely comparable leaf-forms came, for the most part, from geographically limital localities. These data are given below. The total range of the species is shown in a generalized way by the accompanying map (fig. 1).

DATA FROM *Datura meteloides*

Four distinctive groups showing close repetition of leaf-form are listed below. From each group representative collections are cited, chosen from widely separated and geographically peripheral localities. Pen line tracings and map positions are given for each collection.

GROUP ONE (fig. 2)

Leaf-form	*Locality*	*Collector*	*Herb. and sheet no.*
inequilateral ovate and subentire	1. San Bernardino, Calif.	G. R. Vasey 443	USNH 156906
	2. Santa Barbara, Calif.	W. H. Brewer 310	USNH 322527
	3. St. George, Utah	M. E. Jones 6093	RM 14182
	4. Valencia Beach, L. Calif.	Wiggins and Gillespie 3948	USNH 1491044

GROUP TWO (fig. 3)

Leaf-form	*Locality*	*Collector*	*Herb. and sheet no.*
equilateral ovate and serrate	5. Holbrook, Ariz.	Osterhout 6767	RM 169488
	6. Tarrant Co., Texas	A. Ruth 583	USNH 1523537
	7. Fuerte, Sinaloa, Mex.	Rose, Standley and Russell 13452	USNH 636275

GROUP THREE (fig. 4)

Leaf-form	*Locality*	*Collector*	*Herb. and sheet no.*
equilateral ovate and subentire	8. Santa Ysabel, Calif.	Henshaw 68	USNH 238095
	9. Colonia Diaz, Chih., Mex.	E. W. Nelson 6430	USNH 360146
	10. Buckskin Mts., Ariz.	Jones 6063n	USNH 260638

GROUP FOUR (fig. 5)

Leaf-form	*Locality*	*Collector*	*Herb. and sheet no.*
equilateral deltoid and serrate	11. Montezuma Co., Colo.	Crandall in 1895	USNH 963190
	12. Pasadena, Calif.	G. B. Grant 270	RM 54824
	13. Mazatlan, Sinaloa, Mex.	Ortega 5654	USNH 1208683

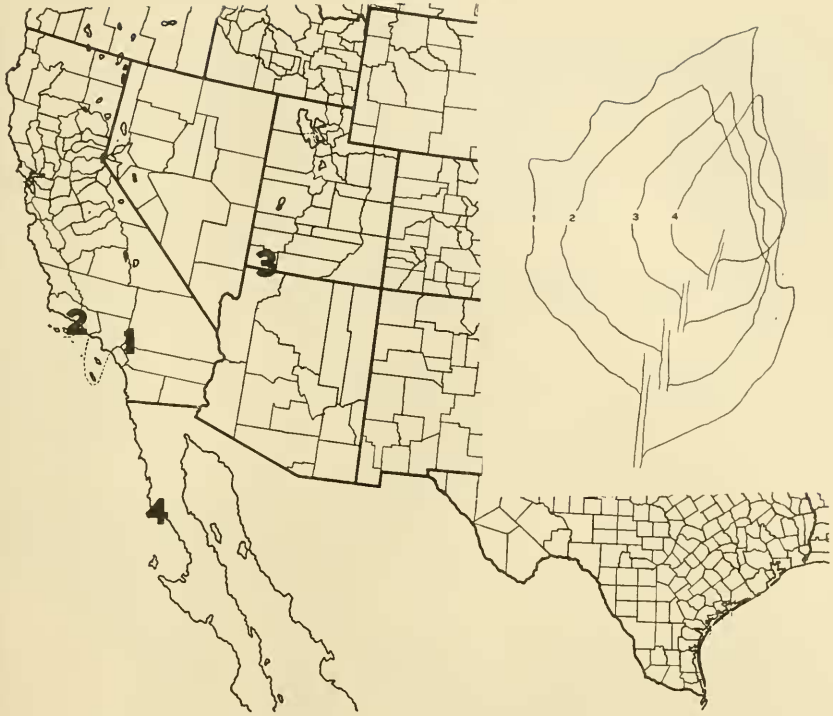

Fig. 2. Group One of *Datura meteloides* leaf-forms.

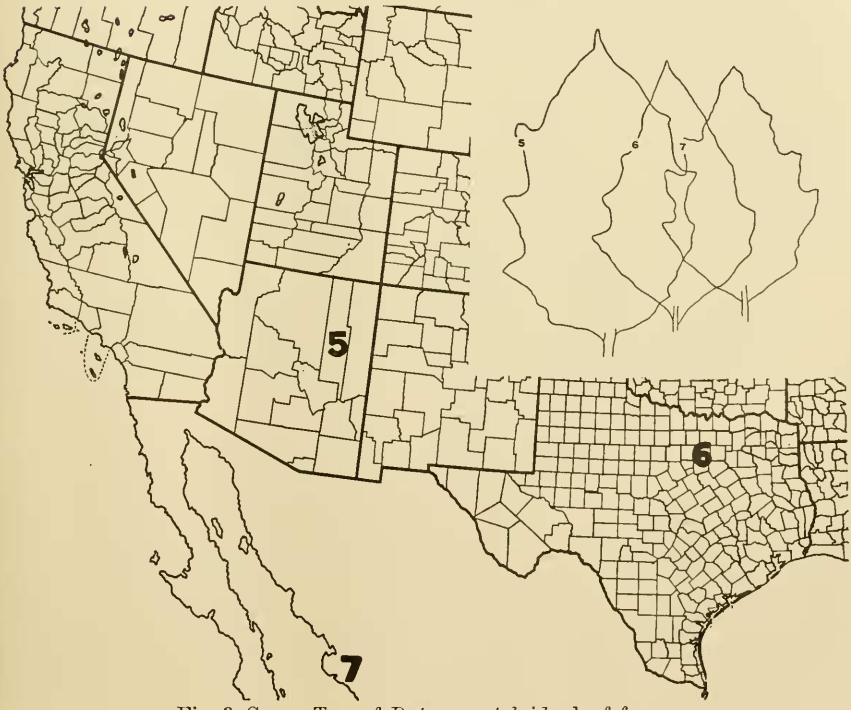

Fig. 3. Group Two of *Datura meteloides* leaf-forms.

Fig. 4. Group Three of *Datura meteloides* leaf-forms.

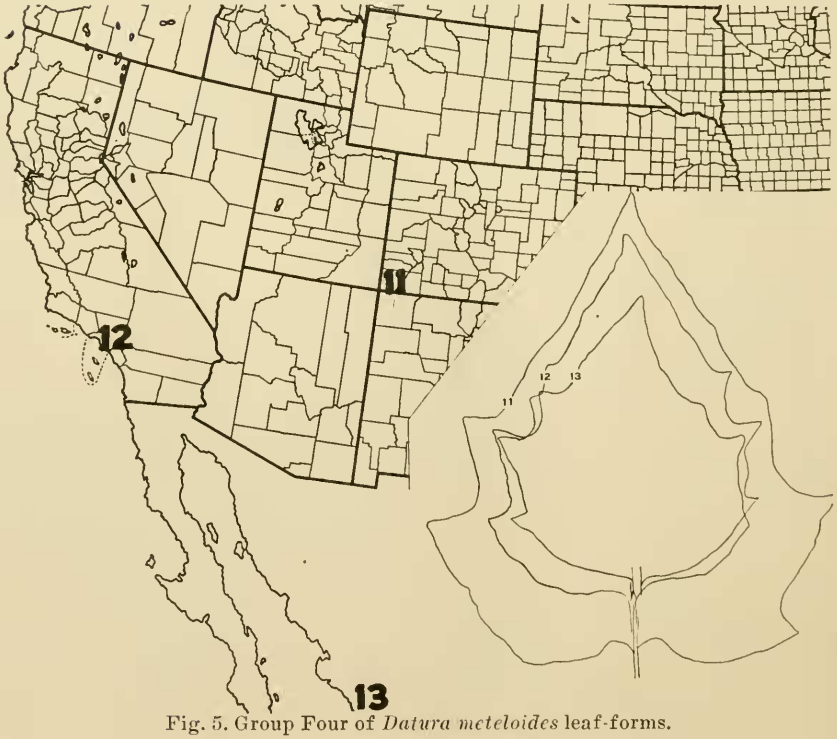

Fig. 5. Group Four of *Datura meteloides* leaf-forms.

Collections from the more central portion of the range of *Datura meteloides* show a range of leaf-forms well represented by the five tracings made from *Charles Wright 526* from Turkey Creek, Texas, which is the lectotype of *Datura Wrightii* Regel (USNH 60043, cf. fig. 6, tracings 14–18 inc. all from same coll.). Collections closely comparable to *Wright 526* in the range of variation of leaf-forms have been made at the stations indicated by the circles

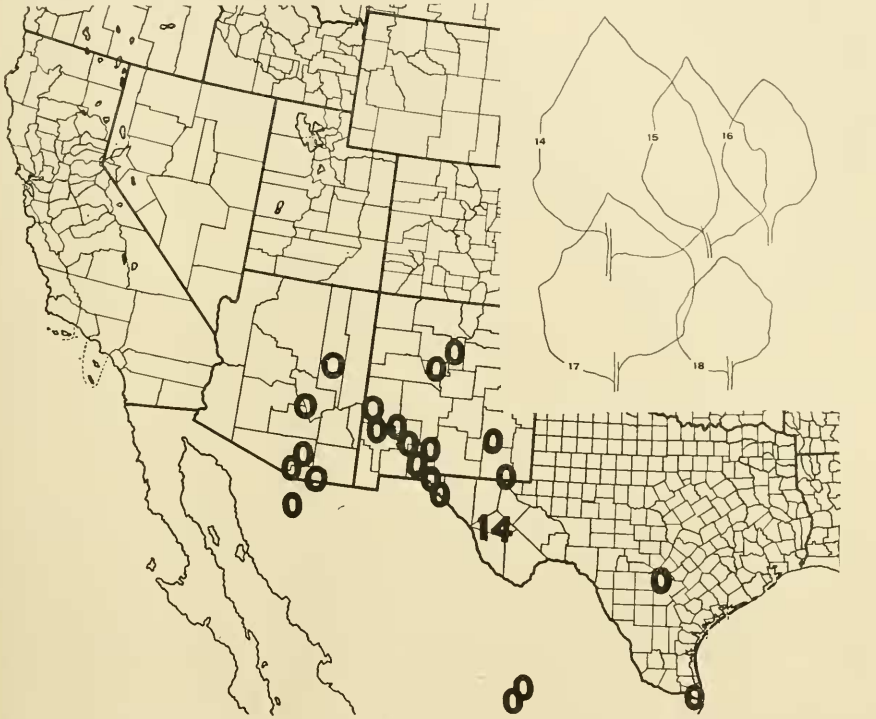

Fig. 6. Center of distribution of *Datura meteloides* as determined by conformity in leaf-form, with five leaves (nos. 14–18) from single coll. (*Wright 526*) from locality at "14."

in fig. 6. This, then, represents the biologic center of the species. Doubtless the species will be found to be present, in suitable river bottom and alluvial habitats, in northern Mexico as well, where the map suggests its absence.

Discussion

The center of distribution for *Datura meteloides* may be recognized as the Rio Grande catchment basin of New Mexico westward to the upper Gila River basin of Arizona. This conclusion is based upon a noticeable homogeneity in the populations as demonstrated by the limited range of variation of their leaf-forms. The peripheral populations are considered, therefore, to represent fragmentary remnants of the original species colony persistent today as a fringe about the now altered population mass comprising the present "center of distribution."

Gleason noted the agreement of marginal members of a group about a center of distribution in his study of the genus Vernonia. He wrote, "that those species most nearly alike morphologically . . . are always distributed about the same center" (1906, 152). C. H. Muller found Matthew's Hypothesis to obtain in certain species of Mexican *Quercus* (oral communication; cf. also *Am. Midl. Nat.* 18: 844, 1937). In my studies of the Californian flora instances which apparently corroborate Matthew's Hypothesis have been noticed in *Monardella lanceolata* Gray, where small capitulae of closely comparable form and size are to be noticed in plants of Yosemite Valley on the north and San Diego County, California, on the south. In the mariposa called "lantern-of-the-fairies," *Calochortus albus* Dougl., closely parallel small-flowered forms may be recognized at almost the same geographically distant localities as in *Monardella*,[1] each an extreme limital population of the species range. Among the North American *Delphiniums*, infraspecific phases have been detected in the Californian *Delphinium Parryi* Gray where small-flowered populations occur, again, at limital positions over the total range of the species. In *Delphinium patens Greenei* (Eastw.) Ewan, a very restricted subspecies of California, plants with identical glandular pedicels occur on Marysville Buttes in the northern Great Valley on the north and from Fresno County upper foothills on the south, with non-glandular plants of *Delphinium patens patens* occupying the intervening area.

An apparent antithesis of Matthew's Hypothesis as valid for *Datura meteloides* occurs in *Tradescantia* where the peripheral populations have been demonstrated by Anderson and Woodson (1935) to be derivitive tetraploid infraspecific races, with the ancestral diploid races occupying the center of distribution. These infraspecific races are indistinguishable in their morphology. The oldest members of the species populations are central, then, and not, as in *Datura meteloides*, marginal to the mass of the species. In *Tradescantia* the center of distribution significantly is geologically an old land mass within the total range of the species. In *Datura meteloides* the peripheral populations occupy extremely diverse regions which are not often cognate geologically. Furthermore, these peripheral populations are not morphologically homogeneous, at least as to their leaf-forms, but differ within themselves from the much more uniform plants of the center of distribution. There are, in fact, four distinctive leaf-forms existing more or less side by side within this marginal population; at least in coastal Southern California three of the four leaf-forms occur together.

In the European crucifer *Biscutella laevigata* L. three polyploid infraspecific races—a diploid, tetraploid and hexaploid race—have been shown to exist by Irene Manton (1937). Here the archaic diploids are "xerothermal" interglacial relicts along the river valleys of central Europe from Germany to the Balkans, north and east of the Alps. The tetraploid plants occupy the

[1] "As is frequently the case with *Labiatae*, the extreme forms geographically are often most similar, at least superficially." (Epling, A Revision of *Salvia:* Subgenus *Calosphace*, 191, 1939).

Swiss and Austrian Alps, swept over by glaciers, as a subsequent invading population. Obviously there is no direct relation to glaciation in the distribution of *Datura meteloides*.

There is, however, with this *Datura* a clear floristic affinity to the Sierra Madrean element of Southwestern United States and Mexico. Axelrod's map (1939, 59, fig. 2B) should be studied in this regard. This map shows the "supposed distribution of the Sierra Madrean element as a dominant" at Lower Pliocene time. This extent agrees very closely with the extreme geographic range enjoyed by *Datura meteloides* at the present time. Indeed, the peripheral populations whose leaves exhibit these four distinctive leaf-forms characterized in the present paper fall very nearly upon the margin of this mapping of the Sierra Madrean floristic element by Axelrod. The only notable exception is the northeastern arm in its range lying to the east of the Llano Estacado of Texas (cf. fig. 1). This arm falls, perhaps significantly, to the east or coastward of the Fall Line, passing northward on the Coastal Plain sediments. The absence of *Datura meteloides* in the region to the west, that is, on the Llano Estacado, is believed by Prof. E. L. Reed to be due essentially to the lack of proper alluvial or river-bottom habitats in that region (personal communication, 22 Feb. 1939).[2] The occupation of the Coastal Plain, and hence, the significance of the Fall Line as marking the upper limit of the Coastal Plain or the "boundary between Triassic and older formations on the inland and Lower Cretaceous (Comanchean) and later formations coastward," has been discussed by Pennell very fully (1935, 572–579).

It will be noted that the marginal phases of *Datura meteloides* today are usually topographically isolated by mountain ranges of varying height and extent or by arid desert expanses with their playas and bolsons, serving as topographic barriers. Topographic isolation, to a degree then, has maintained these distinctive leaf-forms at these limital stations.

Summary

The central populations of *Datura meteloides*, the "tolguacha," though variable, are uniform to a degree and show in general an absence of such leaf-forms as are exhibited by the geographically peripheral populations. There exist on the margin of its range today four leaf-forms; these leaf-form types are not geographically segregated, however, but sometimes occur together in the same marginal locality.

An explanation may be: the population of the original center of distribution was highly heterozygous and consisted of several infraspecific races (this needs cytogenetic confirmation). Applying the concept of Matthew, these several races moved outward in irregular waves of varying intensity and direction and for varying time durations. This movement may have been part of the larger general spread of the Sierra Madrean floristic element over the Southwest. The end result is a series of partial-populations now scattered on

[2] Prof. B. C. Tharp finds no coll. from the Llano Estacado in Univ. Texas Herb.

the periphery of the species range. Each partial-population is reminiscent in its leaf architecture of its descent from a parent race which, as a race, has been lost in the center of the species mass by the subsequent swamping and intermingling of races and the genetic stabilization of the species.

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